



## Spatial synchrony in cisco recruitment



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### ABSTRACT

We examined the spatial scale of recruitment variability for disparate cisco (*Coregonus artedii*) populations in the Great Lakes ( $n=8$ ) and Minnesota inland lakes ( $n=4$ ). We found that the scale of synchrony was approximately 400 km when all available data were utilized; much greater than the 50-km scale suggested for freshwater fish populations in an earlier global analysis. The presence of recruitment synchrony between Great Lakes and inland lake cisco populations supports the hypothesis that synchronicity is driven by climate and not dispersal. We also found synchrony in larval densities among three Lake Superior populations separated by 25–275 km, which further supports the hypothesis that broad-scale climatic factors are the cause of spatial synchrony. Among several candidate climate variables measured during the period of larval cisco emergence, maximum wind speeds exhibited the most similar spatial scale of synchrony to that observed for cisco. Other factors, such as average water temperatures, exhibited synchrony on broader spatial scales, which suggests they could also be contributing to recruitment synchrony. Our results provide evidence that abiotic factors can induce synchronous patterns of recruitment for populations of cisco inhabiting waters across a broad geographic range, and show that broad-scale synchrony of recruitment can occur in freshwater fish populations as well as those from marine systems.

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## 1. Introduction

Separate populations of the same species are frequently observed to fluctuate synchronously (Post and Forchhammer, 2002), yet the mechanisms contributing to these patterns are often unclear. Understanding the spatial scale of synchrony can provide insight into the processes involved because different forcing mechanisms often operate at different spatial scales. For

example, biotic factors (e.g., predation and competition) are generally believed to operate at local scales, while many abiotic factors (e.g., climate) operate at broader scales. The synchronizing effect of environmental factors is referred to as the “Moran effect” (Hudson and Cattadori, 1999). Moran’s theorem states that the spatial correlation of population variation will equal the spatial correlation of environmental variation for those species whose dynamics are driven by similar environmental cues (Moran, 1953).

Sources of recruitment variation in fish populations have been the subject of much debate (Houde, 2008). Analyses by Myers et al. (1997) suggested the spatial scale of recruitment synchrony for marine fishes is approximately 500 km compared to only 50 km for freshwater fishes. Myers et al. (1997) concluded that biotic interactions regulated recruitment of freshwater species while abiotic factors were more important for marine species. While local biotic interactions certainly influence freshwater fish recruitment, the effects of abiotic factors like climate cannot be dismissed. For example, several studies have reported that indices of water temperature were correlated with patterns of walleye (*Sander vitreus*)

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year-class strength (Koonce et al., 1977; Busch et al., 1975; Schupp, 2002). In addition, Phelps et al. (2008) found that climatic variability synchronized recruitment of common carp (*Cyprinus carpio*) across a 175-km<sup>2</sup> area in the Midwestern United States. Marjomäki et al. (2004) analyzed time-series of vendace (*Coregonus albula*) from 21 lakes in Finland (surface areas < 1100 km<sup>2</sup>) and found significant positive correlations among lakes in both recruitment and spawner indices for populations separated by 100–300 km. Bunnell et al. (2010) studied the upper Great Lakes (>50,000 km<sup>2</sup>) and found bloater (*Coregonus hoyi*) recruitment was synchronized at 600–800 km. These authors concluded that dispersal of bloater likely contributed to within-lake synchrony, but climate likely led to synchrony found across lakes because the dispersal mechanism seemed implausible. The inferences of Bunnell et al. (2010) were based on catches of 95–130 mm (age-0 and age-1) bloater, and thus dispersal of smaller bloater from natal areas to other sites in the same lake could not be ruled out. Collectively, these examples provide evidence that the spatial scale of synchrony in freshwater populations often exceeds 100 km, suggesting climate can influence fish recruitment in lacustrine environments.

Climate variables are strongly correlated over broad spatial scales (e.g., >1000 km), especially in terms of mean annual values (Koenig, 2002). However, the magnitude of fish recruitment can be set in short time windows (Cushing, 1990). It follows that measuring spatial synchrony of abiotic factors using mean values that integrate too long a time period may mask the Moran effect. Marjomäki et al. (2004) found that vendace population indices and mean air temperature during the month following ice break-up were anisotropic, meaning patterns of synchrony were more evident along east-west axes than north-south axes. This observation highlights the influence of prevailing weather patterns and their movement across the landscape and also underscores the need to consider both the spatial and temporal aspects of plausible bottlenecks when attempting to understand how climate may influence recruitment.

Another important consideration when trying to understand climate effects is the physical characteristics of the lakes under study. Myers et al. (1997) argued that regional weather systems should affect lakes and streams just as they would marine ecosystems. However, freshwater ecosystems vary extensively in size and shape and thus respond to climatic variables at different rates (Magnuson et al., 1997; Gerten and Adrian, 2001; George et al., 2004). Marjomäki et al. (2004) noted that the date of ice-break between Finnish lakes ranged from less than two to greater than four weeks across years, which highlights the variability that can occur in inland lakes, despite their geographic proximity. In contrast, the thermal inertia, internal currents, and hydrologic connectedness of larger systems, such as the Great Lakes, could lead to a more uniform response to climate through space. Thus, the difference in spatial synchrony for vendace and bloater could be interpreted as species-specific dependences on climatic variables or the heterogeneous response of different types of lakes exposed to similar climate regimes. Given the variability associated with freshwater lakes, broad-scale measures of spatial synchrony are an indication of the role of climate but finer-scale measures do not necessarily preclude the influence of climate.

Cisco (*Coregonus artedii*) are a widely distributed freshwater species in the northern regions of North America and can be found in both the Laurentian Great Lakes and deep inland lakes (Scott and Crossman, 1973). In Lake Superior, cisco begin aggregating in October and spawn primarily during November and December (Stockwell et al., 2009). After hatching, cisco larvae spend their early stages of development near the surface in May and June (Stockwell et al., 2009). There is strong evidence indicating that the year-class strength of cisco and other coregonines is established prior to the end of the larval stage (McCormick et al., 1971;

Viljanen, 1988; Kinnunen, 1997), with the first few weeks after hatching being especially critical (Rice et al., 1987). Bronte et al. (2003) and Stockwell et al. (2009) showed that year-class strength was synchronized across Lake Superior cisco stocks, and concluded that climate drove these patterns. However, neither analysis provided quantitative estimates of spatial synchrony. Thus, our primary objective was to determine the spatial scale of synchrony for cisco within the Great Lakes, and to explore whether inclusion of populations outside the Great Lakes influenced our findings. To evaluate this objective we gathered data for cisco populations covering a broad spatial scale (>1000 km) occupying a range of lake sizes. We coupled this with an analysis of the spatial correlation of spring meteorological observations from offshore Great Lakes weather buoys, which led to the development of hypotheses regarding the potential influence of climatic variables on cisco recruitment. Although the role of climate in determining Lake Superior cisco recruitment has been speculated (Bronte et al., 2003; Stockwell et al., 2009), Bunnell et al. (2010) highlighted that it is wrong to assume population synchrony is driven solely by climatic events when dispersal of individuals could also explain the phenomenon. To better understand whether dispersal or climate drives cisco synchrony, we examined the inter-annual variability of larval cisco densities at three Lake Superior sites that were separated by 25–275 km. Finding spatial synchrony of larvae that were collected concurrently at separate sites within weeks of emergence would provide evidence that climate, and not dispersal, led to patterns observed by Bronte et al. (2003) and Stockwell et al. (2009).

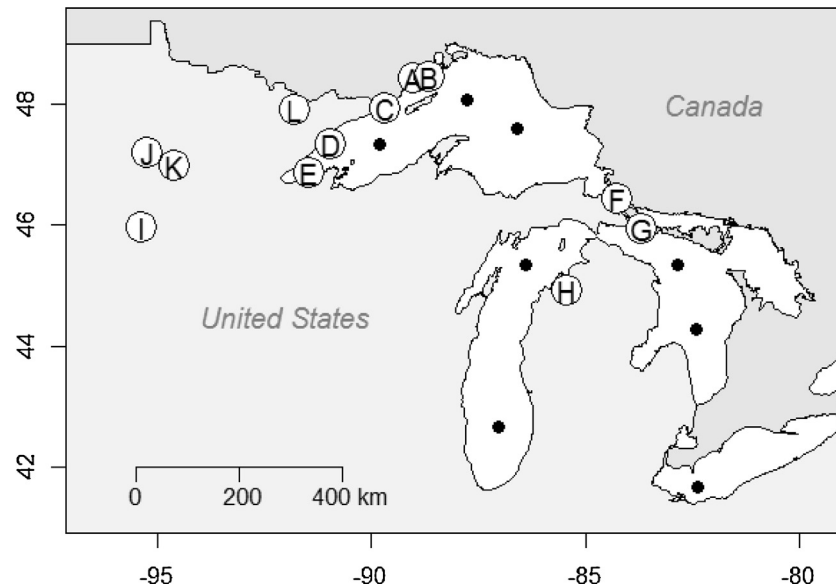
## 2. Methods

### 2.1. Acoustic data collection and sample processing

We sampled 12 cisco populations across the upper Great Lakes region (Fig. 1) including 5 sites in Lake Superior, 2 sites in Lake Huron, 1 site in Lake Michigan, and 4 small lakes in northern Minnesota. Populations in the Great Lakes were assessed during November 2010 when cisco were aggregated for spawning (Yule et al., 2009), while populations in the Minnesota inland lakes were assessed during July and August 2010 (Ahrenstorff et al., 2013). The objective of both the autumn and summer surveys was to measure abundance of yearling and older pelagic fish so combining these datasets was deemed appropriate.

Stockwell et al. (2009) showed that bottom trawl surveys do not adequately describe the age structure, density, or biomass of cisco in Lake Superior. Thus, night hydroacoustic surveys were coupled with netting to estimate abundance and characterize size and age structures of each population. Acoustic data collection and processing followed the Great Lakes standard operating procedure (Parker-Stetter et al., 2009; Rudstam et al., 2009). We collected between 6 and 131 km of acoustic data at each site, with indices of coverage (Aglen, 1983) ranging from 1.2 to 5.0 (Table 1). Using Echoview software version 4.90 (Myriax Pty Ltd., Tasmania, Australia), we defined cells on echograms measuring 10 m in height by 2 km in length and calculated total fish densities (#/ha) in each cell from 3 m below the surface to 0.5 m above the lakebed. Target strength (TS) distribution exports for each cell were used to estimate densities of two sizes of fish: small fish < −35.6 decibels (dB), and large fish ≥ −35.6 dB, coinciding to fish less than and greater than 250 mm, respectively (Yule et al., 2006, 2009). At Drummond Island the acoustic data from 2010 were compromised due to electrical interference, so we used acoustic data gathered during October 2009 for this site.

Midwater trawl catches were used to interpret acoustic data at Lake Superior sites, while gillnets were used at the much shallower Lake Huron, Lake Michigan, and Minnesota inland lake sites



**Fig. 1.** Locations of cisco populations (letters) and NOAA buoy stations (black dots) used to test the scale of spatial synchrony within the region. The letters in this map correspond to the letters used in other tables and figures.

(Table 1). The gear deployed at each site (Table 1) was capable of catching yearling and older cisco. All captured fish were sorted to species and counted. We measured total length of all fish from most sites, but did sub-sample some large catches of non-target species. Fish that were not measured were assigned a total length based on the measurement of  $\geq 50$  randomly selected fish of the same species.

Yule et al. (2013a) used simulated fish communities to demonstrate that classification trees performed well as an acoustic apportionment method. For this reason we developed classification tree models (*sensu* Yule et al., 2013b) using the recursive partitioning package (Therneau and Atkinson, 2012) available in R (R Development Core Team, 2011). Separate trees were developed for both large ( $\geq 250$  mm) and small fish ( $< 250$  mm) caught at each site in the Great Lakes. This size threshold and the associated TS cut-off (i.e.,  $-35.6$  dB) have been used to separate mature cisco from smaller pelagic fish (e.g., rainbow smelt (*Osmerus mordax*), juvenile cisco) during previous surveys of cisco populations in Lake Superior (Yule et al., 2006, 2009). Cisco caught in the Minnesota lakes

were all smaller than 250 mm (Ahrenstorff et al., 2013), leading us to develop a single classification tree for each inland lake. Species was the response variable while latitude, longitude, bathymetric depth, and depth of capture were potential explanatory variables. The number of samples collected and the characteristics of certain sampling approaches negated the use of some explanatory variables. For example, locations where only a single sample was collected negated use of latitude and longitude while use of only bottom-set gillnets negated use of capture depth. Trees were first constructed using a liberal complexity parameter (0.0001) and then pruned back based on the cross-validation error associated with each of the splits. We chose the smallest tree in which the point estimate of cross validation error fell within one standard error of the minimum cross validation error (Zuur et al., 2007). In addition, terminal leaves with  $< 10$  fish were pruned (Yule et al., 2013a, 2013b). The species proportions of the model terminal leaves were used to apportion the cell density estimates to species (*sensu*, Yule et al., 2013a). If the model could not find a meaningful split of the data, we used the species proportions from all catches at a given site to

**Table 1**

Sampling date(s), area sampled ( $\text{km}^2$ ), kilometers (km) of acoustic data collected, degree of coverage, sampling gear, and number of samples collected to survey cisco populations across the upper Great Lakes region. Sampling dates are for the year 2010, with the exception of Drummond Island, for which acoustic data were collected in 2009. The gear used to sample cisco included midwater trawls (MWT; 15.2 m headrope and footrope lines; 13.7 m breast lines; 152 mm mesh at the mouth graduated to 13 mm at the cod end), bottom-set gillnets (BGN; graded-mesh, multifilament; 50.8–101.6 mm stretch measure in 12.7 mm increments), and vertical-set gillnets (VGN; graded-mesh monofilament gillnet; 9.5, 12.7, 19.0, 31.8 and 50.8 mm stretch measure).

Location	Area ( $\text{km}^2$ )	Date(s)	Acoustic data (km)	Degree of coverage	Gear (# samples)
<i>Lake Superior</i>					
(A) Thunder Bay	700	11/09–11	131	5.0	MWT (14)
(B) Black Bay	300	11/12–13	82	4.7	MWT (7)
(C) Grand Portage	100	11/14	24	2.4	MWT (4)
(D) North Shore	100	11/08–09 and 11/15–17	12	1.2	MWT (7)
(E) South Shore	300	11/16	65	3.8	MWT (7)
<i>Lake Huron</i>					
(F) St. Mary's River	5	11/03	9	2.2	BGN (4)
(G) Drummond Is.	10	10/15	14	3.1	BGN (3)
<i>Lake Michigan</i>					
(H) Grand Traverse Bay	5	11/09	8	2.2	BGN (15)
<i>Minnesota</i>					
(I) Carlos Lake	10.2	08/09	14	4.4	VGN (1)
(J) Elk Lake	1.1	08/03	6	5.7	VGN (1)
(K) Ten Mile Lake	20.4	07/19	14	3.1	VGN (1)
(L) White Iron Lake	6.9	07/28	7	2.7	VGN (1)

apportion acoustic densities. We summed cisco density estimates across all cells in each 2-km segment and calculated an average density of small and large cisco (where applicable) using the 2-km segments as sample units.

## 2.2. Estimating year-class strength

Cisco were aged by one individual at North Shore Environmental Services (Thunder Bay, Ontario) using the crack and burn method of aging otoliths (Schreiner and Schram, 2001). Yule et al. (2008) showed that this age using this method provided age estimates consistent with a Lake Superior recruitment index. We assigned ages to all cisco caught at each site using site-specific semi-random age-length keys (Ogle, 2012) constructed with 50 mm length bins. After assigning each captured cisco an age estimate, we assumed the catch at each site reflected the true population, and apportioned the average density of small and large cisco measured at each site to age classes.

Stockwell et al. (2009) used a von Bertalanffy growth curve to show that age-1 cisco caught in the Apostle Islands region of Lake Superior during November and December were approximately 150 mm. In addition, Yule et al. (2006) demonstrated that the majority of cisco collected using midwater trawls during a 2004 spawning assessment in the Apostle Islands were immature (i.e., 138–238 mm). The 2003 cisco year-class was deemed successful in Lake Superior (Stockwell et al., 2009), providing evidence that age-1 and older cisco were vulnerable to our midwater trawl gear. Furthermore, graded-mesh gillnets have been used to characterize the size structure of cisco >100 mm (Ahrenstorff et al., 2013) so we assumed both gears provided an unbiased assessment of the populations.

A weighted catch-curve regression (Maceina and Bettoli, 1998) was fit to the age-specific, natural log (ln) transformed densities (i.e., age-1 to the maximum observed age) of each population and the relative strength or weakness of each year-class was defined by the studentized residual. A weighted regression was used for the analysis because cisco can live in excess of 20 years and exhibit spasmodic recruitment (Yule et al., 2008). Older and rarer cohorts are often underrepresented when sample size is low and thus, the influence of these cohorts is deflated by conducting an initial regression and using the predicted values of ln-transformed densities for each age as weights for a second regression procedure (Maceina and Pereira, 2007). Using Pearson product moment correlation coefficients, we compared the catch-curve residuals for each possible pairing of locations to determine whether population fluctuations were synchronous.

## 2.3. NOAA buoy observations

Climate and limnological data were obtained from eight offshore buoy stations in Lakes Superior, Michigan, Huron, and Erie (Fig. 1) operated by the U.S. National Oceanic and Atmospheric Administration (NOAA). We used records between May 15 and June 15 for the years 1983–2010 because Lake Superior larval cisco emergence generally peaks during this period (Hatch and Underhill, 1988; Myers et al., 2009), and fish from the 1983 to 2010 year-classes were represented in our 2010 age estimates. When there were multiple recordings for a single day, we used the average of the measurements for that day. We calculated the Pearson product moment correlation coefficient for each possible pair of buoy stations using the annual time series of average air temperature, average surface water temperature, average wind speed, and maximum wind speed.

## 2.4. Estimating the spatial scale of synchrony for cisco recruitment and climatic factors

We followed the methods of Myers et al. (1997) in their global, multi-species meta-analysis in order to ensure comparability of results. According to Myers et al. (1997), a simple estimate of the spatial scale of synchrony is the distance over which the pairwise correlation coefficients between recruitment (defined as the catch-curve residuals) or climate time-series is reduced by a factor  $e^{-1}$ , (i.e., the exponential decay rate or the  $e$ -folding scale; Myers et al., 1997). Using iterative least squares, we fit the following model:

$$\rho(d) = \rho_0 e^{-(d/v)},$$

where  $\rho_0$  is the correlation between two stocks at zero separation,  $v$  is the  $e$ -folding scale, and  $d$  is the straight-line distance (km) between populations or buoys. The parameter  $d$  was measured by first converting coordinates from decimal degrees to UTM, which allowed us to calculate the distance between the two points using the Pythagorean theorem. In this model, we constrained  $\rho_0$  to have an absolute value of 1 or less. To take into account that some correlation-distance relationships might have a “shoulder” at  $d=0$ , we also fit the following model developed by Myers et al. (1997):

$$\rho(d) = \rho_1 e^{-0.5(d/\sigma)^2}$$

where  $\sigma$  is a fitted parameter, analogous to  $v$ , above. Pairwise correlations for cisco recruitment were only included when two populations had at least five year classes in common. Comparing the spatial scale of synchrony for cisco populations to that of environmental variables guided our evaluation of potential factors driving cisco recruitment in the region.

## 2.5. Evaluating the role of dispersal in Lake Superior

Inclusion of data from four Minnesota inland lakes allowed us to evaluate the hypothesis that dispersal might be the mechanism responsible for synchrony of recruitment. To further consider this possibility we examined larval cisco densities collected over five years (2006–2011) at three Lake Superior sites (Thunder Bay, Black Bay, and South Shore; Fig. 1), separated by 25–275 km. These data were collected as larvae emerged at each site, so dispersal between sites could not explain any observed co-variation. An individual sample consisted of measuring larval densities (No. per 1000 m<sup>3</sup>) at individual stations (~1 station per 1000 ha, see Myers et al., 2009 for example survey designs) using the capture methods of Myers et al. (2008). Only samples collected between May 15 and June 15 were used in the analysis because it is the period when the majority of cisco had hatched. Due to logistical constraints, all sites were not sampled in all years. An ANOVA model was used to determine whether the ln-transformed larval cisco densities varied with respect to year, site, or the interaction between year and site. Tukey's multiple comparison procedure was used to interpret significant differences identified by the ANOVAs. Prior to transformation, we added the minimum density observation greater than zero to all density estimates from the given location. Evidence of a significant main effect of year, and the absence of a significant year-by-site interaction would suggest that a common factor was influencing larval density among these sites.

## 3. Results

The apparent synchrony in cisco recruitment across the region seems to be largely due to high recruitment during some years (e.g., 2009) and low recruitment during others (e.g., 2006) (Figs. 2 and 3). In Lake Superior and Lake Huron, synchrony appears to be the result



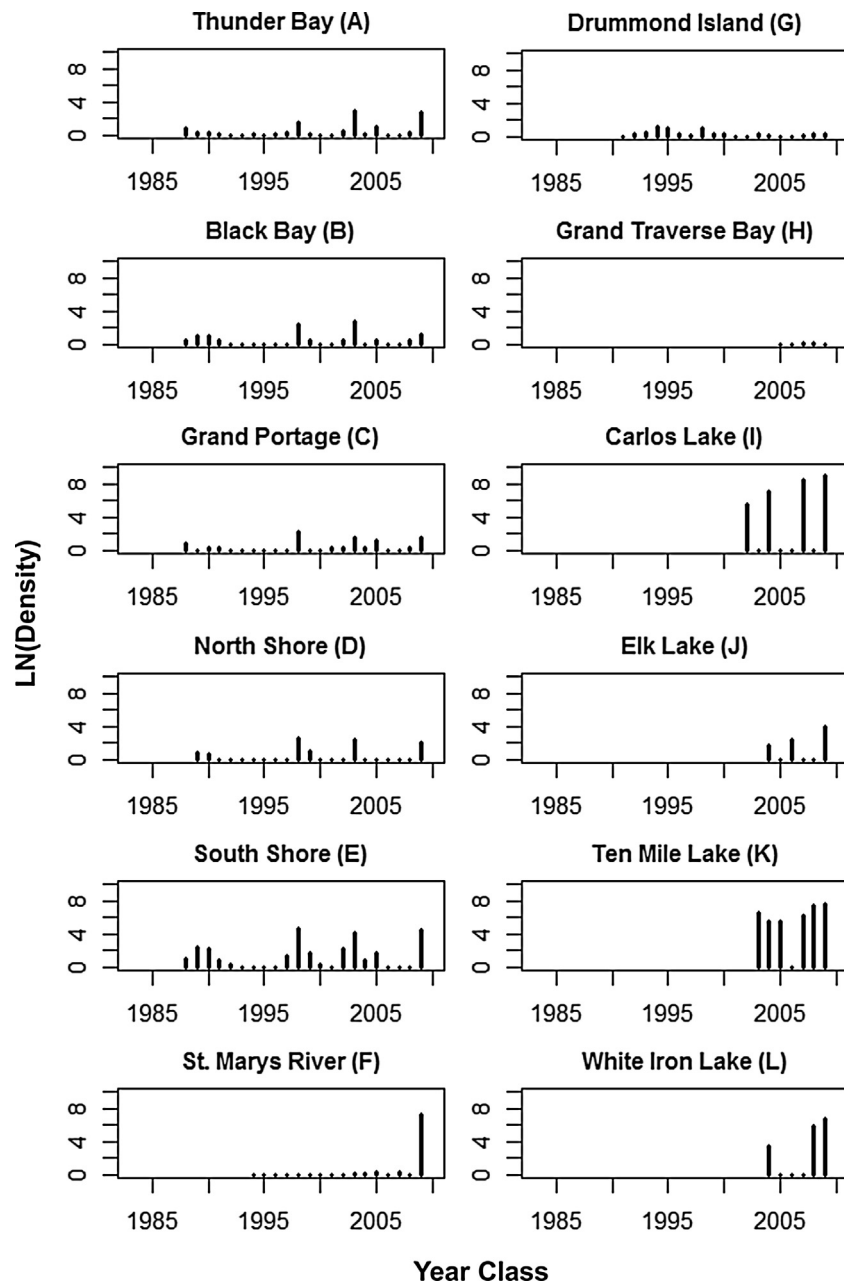


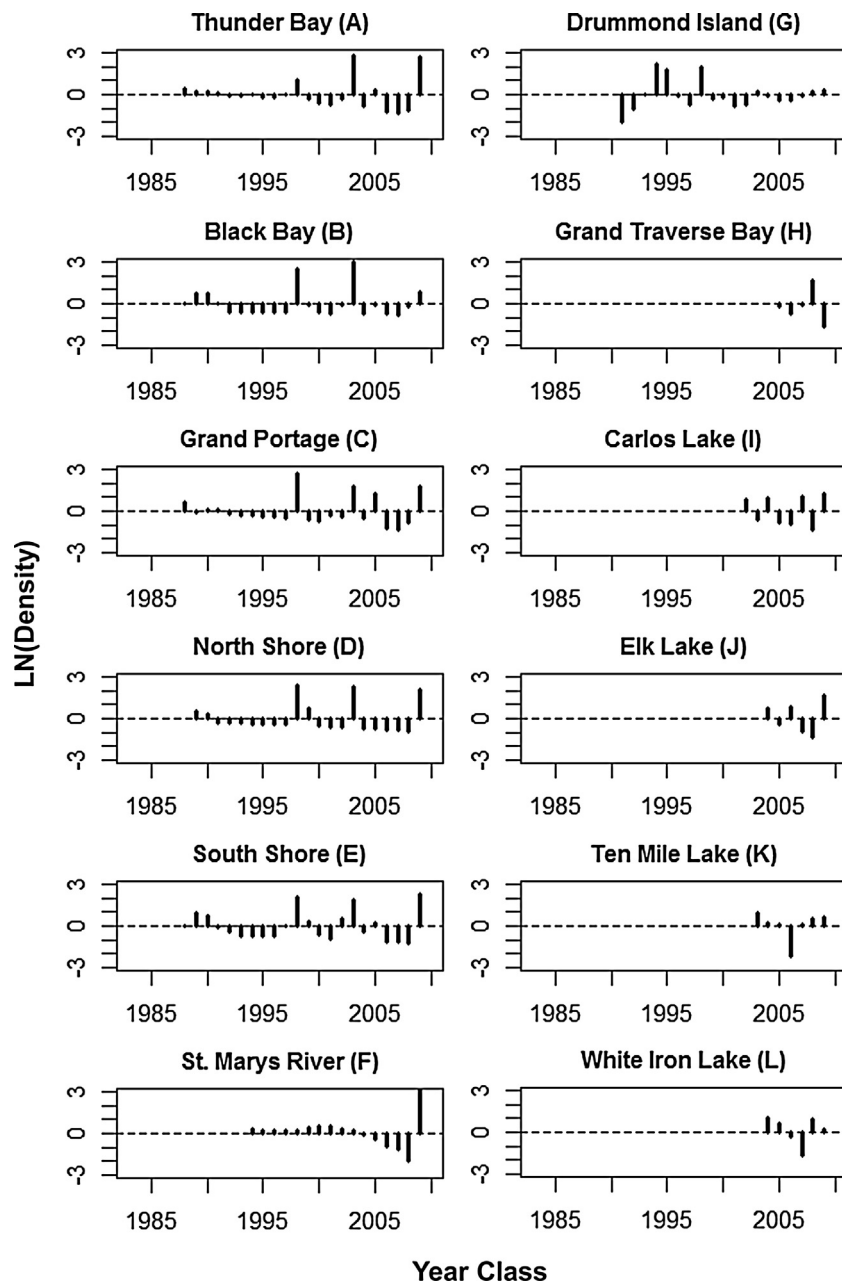
Fig. 2. Ln-transformed density (#/ha) of individual cisco year-classes at sites in the Great Lakes (A–H) and Minnesota inland lakes (I–L).

of predominately poor recruitment in conjunction with occasional strong year-classes (e.g. 1998, 2003). Although populations in Lake Superior and Lake Huron were characterized by infrequent recruitment, they appear to have greater longevity ( $\geq 15$  years) than cisco in Lake Michigan and the Minnesota inland lakes ( $\leq 8$  years) investigated (Fig. 2).

The exponential fit between distance and the decay of the pairwise correlation of the residuals from the catch curves showed that the e-folding scale for populations in the Great Lakes was 245 km (SE=135) to 236 km (SE=83), depending on the model (Fig. 4, Table 2). Meanwhile, when cisco populations from both the Great Lakes and Minnesota inland lakes were combined the e-folding scale was 468 km (SE=234) to 359 km (SE=99), which suggests that inclusion of inland lake cisco populations did not lower estimates of spatial synchrony. The variation in correlation coefficients was large and contained a considerable number of negative

values, yet these results are consistent with those presented by Myers et al. (1997) for marine species. Many of the negative values were the result of comparisons between Grand Traverse Bay and other populations (Fig. 4), which suggests recruitment dynamics at Grand Traverse Bay were unique. When comparisons with Grand Traverse Bay and Minnesota inland lakes were excluded, the spatial scale of synchrony for the remaining cisco populations in the Upper Great Lakes was 724 km (SE=259) to 431 km (SE=69).

Correlations between average spring (May 15–June 15) air temperature, surface water temperature, or wind speed and buoy separation distance generally declined in a linear fashion, while maximum wind speed declined exponentially (Fig. 5). The correlation scale (i.e.,  $\sigma$ ) is greater than 800 km for average spring air temperature, water temperature, and wind speed (Table 2). However, the correlation scale of maximum wind speed was only

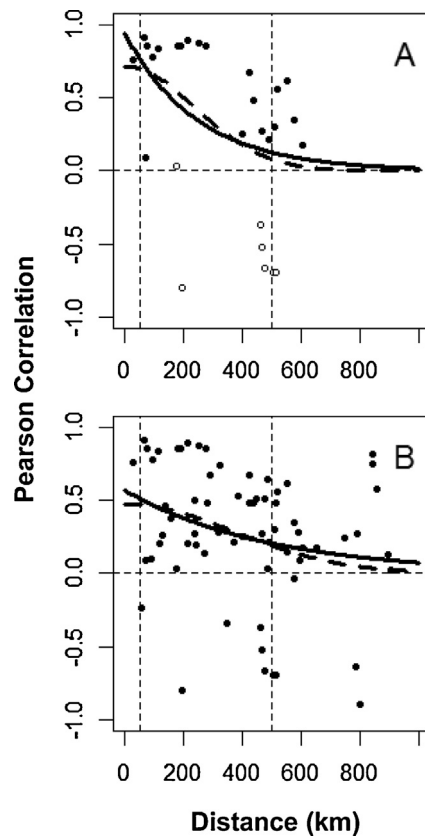


**Fig. 3.** Residuals from catch-curve regressions, which serve as indexes of year-class strength for cisco populations in the Great Lakes (A–H) and Minnesota inland lakes (I–L).

**Table 2**

Parameter estimates and their standard errors (SE) for the two models used to describe the spatial scale of correlation of cisco recruitment and meteorological data. The meteorological variables that were investigated include average air temperature, average water temperature, average wind speed, and maximum wind speed. Observations are from May 15 to June 15 for the years 1983–2011.

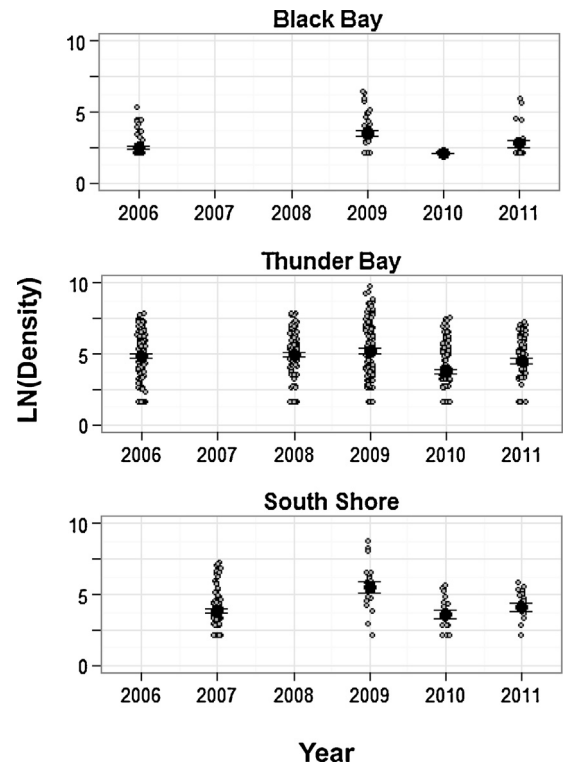
Data	$\rho_0 e^{-(d/\nu)}$				$\rho_1 e^{-0.5(d/\sigma)^2}$			
	df	RSE	$\rho_0$ (SE)	$\nu$ (SE)	df	RSE	$\rho_1$ (SE)	$\sigma$ (SE)
<i>Cisco recruitment</i>								
Great Lakes	26	0.52	0.95 (0.36)	245 (135)	26	0.52	0.73 (0.21)	236 (83)
All Lakes	64	0.44	0.58 (0.18)	468 (234)	64	0.44	0.48 (0.11)	359 (99)
<i>Meteorological variables</i>								
Average air temperature	26	0.16	0.85 (0.09)	2499 (1397)	26	0.16	0.80 (0.05)	983 (231)
Average water temperature	26	0.12	0.94 (0.07)	1938 (617)	26	0.12	0.86 (0.04)	911 (136)
Average wind speed	26	0.13	0.67 (0.07)	1553 (644)	26	0.13	0.59 (0.05)	853 (192)
Maximum wind speed	26	0.25	0.68 (0.25)	396 (181)	26	0.26	0.45 (0.13)	388 (114)



**Fig. 4.** Spatial scale of synchrony between pairs of cisco populations in the Great Lakes (A) and also for pairs of cisco populations in the Great Lakes and Minnesota inland lakes (B). Fits of the models  $\rho_0 e^{-(d/v)}$  (solid curve) and  $\rho_1 e^{-0.5(d/\sigma)^2}$  (broken curve) suggest the scale of spatial synchrony extends to approximately 240 km for Great Lakes populations and to 400 km when all available populations were included in the analysis. According to Myers et al. (1997), the expected scale of spatial synchrony for freshwater and marine species is 50 km and 500 km (vertical dashed lines), respectively. Horizontal dashed line represents zero correlation. Open circles in “A” show comparisons between the Grand Traverse Bay cisco population and other Great Lakes cisco populations.

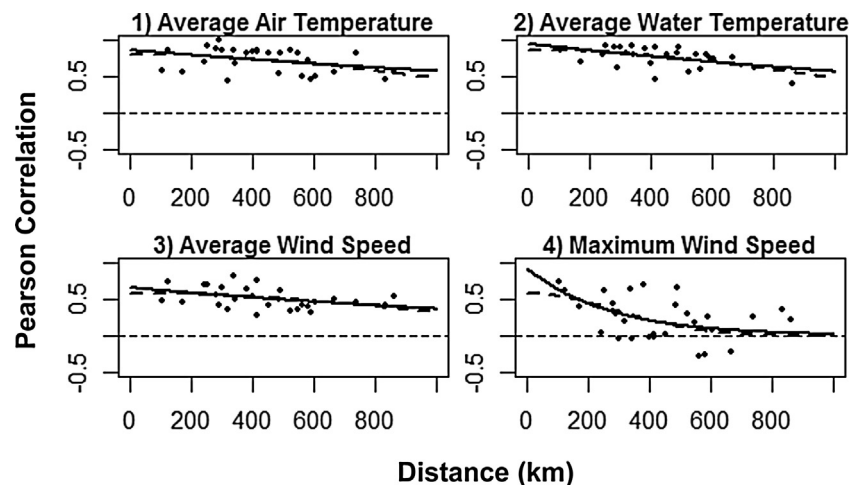
388 km, quite similar to the estimate of  $\sigma$  for cisco recruitment (Table 2).

Larval densities varied significantly ( $p < 0.001$ ) according to year and site (Fig. 6), but the interaction of year and site was not



**Fig. 6.** Ln-transformed larval cisco density during spring emergence (15 May–15 June) at three locations in Lake Superior. Bold points indicate the mean and error bars are 1 SE. Raw data points are offset horizontally for visual purposes. Years with no sampling effort are blank.

significant. Thunder Bay had significantly greater average larval densities than both the South Shore and Black Bay sites ( $p < 0.001$ ), and mean densities at South Shore exceeded that of Black Bay ( $p < 0.003$ ). Compared to the other five years when sampling occurred, larval densities were highest in 2009 ( $p < 0.001$ ). This result is consistent with our age estimates of yearling and older cisco at these three Lake Superior sites (Figs. 2 and 3) which, together with the observed covariation in larval densities among these sites, raises doubt that dispersal drives patterns of spatial synchronicity.



**Fig. 5.** Correlation of (1) average air temperature (2) average water temperature (3) average wind speed and (4) maximum wind speed between pairs of NOAA's Great Lakes buoys versus distance. Observations are from May 15 to June 15 for the years 1983–2011. Models used to estimate spatial scale of synchrony include  $\rho_0 e^{-(d/v)}$  (solid curve) and  $\rho_1 e^{-0.5(d/\sigma)^2}$  (broken curve). Horizontal dashed line represents zero correlation.

#### 4. Discussion

Ecologists have largely accepted that populations of many species fluctuate in synchrony over broad spatial scales (Ranta et al., 1998; Liebhold et al., 2004). Despite general acceptance, there is less agreement about the mechanisms driving the phenomenon. The two major factors hypothesized to be involved in synchronization of the dynamics of disparate populations are climate and dispersal (Koenig, 1999). Our study attempted to separate the effects of dispersal from those of the Moran effect by examining the synchrony of cisco recruitment for populations both within and outside the Great Lakes. We identified substantial synchrony in the recruitment dynamics of cisco across a broad spatial range and believe our argument for the Moran effect is strengthened by the inclusion of populations for which dispersal is not possible. In addition, the positive relationship between larval cisco density and subsequent year-class strength at Lake Superior sites separated by approximately 250 km is further evidence against dispersal being the cause of synchronous recruitment patterns. However, it needs to be mentioned that pelagic fish larvae in the Great Lakes can be transported distances >120 km (Dettmers et al., 2005). Furthermore, cisco larvae in Lake Superior may be transported great distances from major spawning sites by longshore currents (Oyadomari and Auer, 2008). While the role of dispersal cannot be ruled out completely, we believe our results suggest that factors that have a similar influence on geographically disjunct populations are the more probable cause of spatial synchrony in cisco recruitment.

Our estimates of the model parameters provide evidence that the e-folding scale for cisco recruitment (Table 2) likely exceeds what Myers et al. (1997) would have predicted for a freshwater species. Myers et al. (1997) argued that variability in freshwater fish recruitment depends predominately on biotic influences operating at fine scales, while recruitment of marine species is largely determined by environmental factors operating at much broader scales. However, only five freshwater species were considered by Myers et al. (1997) and it is unclear whether the populations were from the Great Lakes or inland lakes. We hypothesize that the size of the system in which a population resides plays a more important role in the recruitment process than salinity. Lakes in the Laurentian Great Lakes and Precambrian Shield Region respond strongly to climate (Magnuson et al., 1997), yet differences in morphometry, hydrology, and other physical factors all contribute to systems responding uniquely. For example, smaller lakes will have a shorter fetch, less consistent mixing currents and less thermal inertia, while larger systems will be characterized by longer fetch, stronger currents and more thermal inertia. For this reason the Great Lakes behave much like inland seas and exhibit physical processes characteristic of the coastal regions of oceans (Rao and Schwab, 2007). Thus, we believe the conclusions of Myers et al. (1997) could be misleading and that lower measures of spatial synchrony associated with freshwater species could simply be an artifact of the heterogeneity of individual ecosystems and their differential response to abiotic factors.

Our estimates of the correlation scale for recruitment of cisco were similar to the results of Rook et al. (2012), which projected that the spatial scale for modeling stock-recruitment dynamics of cisco in Lake Superior was approximately 260 km. However, the analysis by Rook et al. (2012) did not explicitly measure how the correlation between stocks weakened with distance, making comparisons to the global analysis by Myers et al. (1997) difficult. Instead, their inferences were based on the stock-recruitment relationships developed for regions across Lake Superior using density estimates derived from spring bottom trawl samples. There are at least five recent papers in the fisheries literature documenting that day bottom trawl sampling provides estimates of adult cisco abundance that are biased low (Johnson et al., 2004; Mason et al., 2005;

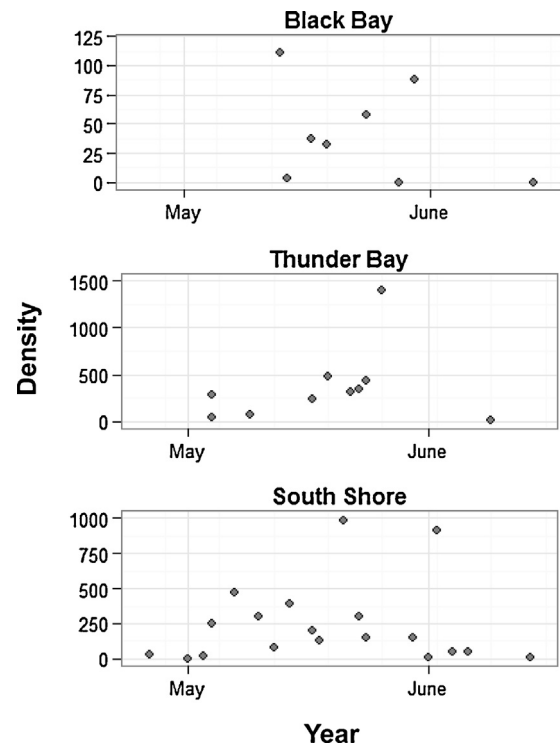


Fig. 7. Average densities (#/1000 m<sup>3</sup>) of larval cisco versus the average date of sampling for surveys conducted at three locations in Lake Superior. Surveys were conducted between 2006 and 2011.

Stockwell et al., 2006; Yule et al., 2007; Stockwell et al., 2009). Stockwell et al. (2006) went on to conclude that earlier attempts to develop stock-recruitment relationships using spring bottom trawl estimates (e.g., Hoff, 2004) were wrong because the sampling approach lacked the precision necessary to develop meaningful relationships (*sensu* Walters and Ludwig, 1981). Stockwell et al. (2006) also argued that Hoff's (2004) search for factors other than adult stock biomass (e.g., lake trout (*Salvelinus namaycush*) abundance, slimy sculpin (*Cottus cognatus*) biomass, April wind speeds) to explain cisco recruitment was undermined by the use of an inappropriate sampling gear, leading to results that were "tenuous at best". Recently, Rook et al. (2013) used an approach similar to Hoff (2004) and found an effect of April wind speed (i.e., during the spring when cisco begin hatching) and April air temperatures (i.e., when cisco are 11–12 months of age) on measures of cisco recruitment from bottom trawls. Having conducted extensive larval sampling in Lake Superior over several years, it has been our experience that cisco are not captured in surface waters until the month of May (Fig. 7), which calls into question how unhatched cisco could be influenced by April winds. Furthermore, the magnitude of cisco recruitment is believed to be established before cisco reach age-1 (Stockwell et al., 2009), meaning the effect of April air temperatures on cisco that are already age-1 is likely trivial. Yule (1926) demonstrated that we sometimes get "nonsense-correlations" between time-series, for which we cannot provide a reasonable defense for how the relationship arose. To advance our understanding of cisco population dynamics in the Great Lakes, we suggest that analyses be based on regular acoustic surveys rather than demersal trawling.

We found that 2009 larval cisco densities were an indicator of subsequent year-class strength, which suggests that processes operating prior to the end of the larval-stage may be important. Houde (1994) argued that differences between the averaged vital rates (e.g., growth rates, mortality rates) and energetics of fish larvae (Houde and Zastrow, 1993) suggests that juvenile-stage



dynamics are more important in determining recruitment levels and variability of freshwater species, while larval-stage dynamics are more important in marine species. Contrary to the results of Houde (1994), evidence suggests year-class strength of coregonines is largely determined during the first few weeks after larval hatching in both European (Viljanen, 1988; Huusko and Sutela, 1998; Auvinen et al., 2000) and North American (Taylor and Freeburg, 1984; Rice et al., 1987; Oyadomari and Auer, 2007) freshwater lakes. Compared to older stages of development, cisco larvae are disproportionately vulnerable to subtle changes in temperature (McCormick et al., 1971) and wind driven currents (Oyadomari and Auer, 2008), which is consistent with the observations of this study. Sensitivity to these factors is compounded by the fact that spring (i.e., period of larval cisco emergence) is usually characterized by higher wind speeds and variable temperatures (Rao and Schwab, 2007).

Our findings suggest that the generalizations of Houde (1994) and Myers et al. (1997) might not apply to all freshwater species and systems. Classification of species and their recruitment dynamics based on whether they inhabit marine or freshwater ecosystems is just one approach. An ecological classification (e.g., Balon, 1975) that considers the early life history of species and the environments they inhabit may provide greater insight about factors that regulate recruitment, particularly across space. Although studies that examine the effects of physical processes on fish recruitment have been more common in the marine literature, the Great Lakes and other freshwater systems provide ample opportunities for similar research. A greater appreciation of physical–biological coupling and recruitment variability will be invaluable for attempts to develop integrated, ecosystem based fisheries management strategies (Ludsin et al., 2014).

It is plausible that a calm spring could lead to more stable environmental conditions (Rao and Schwab, 2007) and therefore reduce the likelihood of larvae being advected to colder and less productive offshore waters (Zhao et al., 2009). A warmer environment would encourage greater production of zooplankton (Shuter and Ing, 1997; Stockwell and Johannsson, 1997) and ultimately increase rates of age-0 cisco development. In general, larvae that obtain larger sizes have greater swimming capabilities, are more successful at feeding, are more resistant to starvation, and are less susceptible to predation (Miller et al., 1988). Based on the time-series of spring maximum wind speeds in western and central Lake Superior, two years with the least severe spring wind events were 1984 and 2003 (Fig. 8). Interestingly, two of the largest cisco year-classes in Lake Superior recruited during these same years (Stockwell et al., 2009). The 1998 cisco year-class was also large, yet the maximum wind event that spring was moderate compared to other years (Fig. 8). However, temperatures during the spring of 1998 were also high (Fig. 8), which could have ameliorated the effect of moderate wind. The 2009 cisco year-class was also successful (Figs. 2 and 3) and the maximum wind event occurred on May 16 during the spring of that year. After that date, the maximum average daily wind speed was 7.0 km/h. Based on our 2009 sampling in Thunder Bay, we found that larval cisco densities were 486/1000 m<sup>3</sup> (SE = 113) and 1399/1000 m<sup>3</sup> (SE = 321) on May 19 and May 26, respectively. Similarly, larval cisco densities along the South Shore in 2009 were 3/1000 m<sup>3</sup> (SE = 2) on May 1 and 981/1000 m<sup>3</sup> (SE = 468) on May 21. Based on this information, we speculate that the strong wind events of 2009 may have occurred prior to the bulk of hatching and thus few age-0 cisco were vulnerable to surface currents at that time. In contrast, strong wind events occurred on May 5 (9.2 km/h) and then again on May 25 (9.4 km/h) during the spring of 2007. Eight synoptic surveys were conducted along the South Shore in 2007 between April 26 and June 14, yet larval cisco densities never reached the levels observed in 2009 (Fig. 6). This information leads us to conclude that any

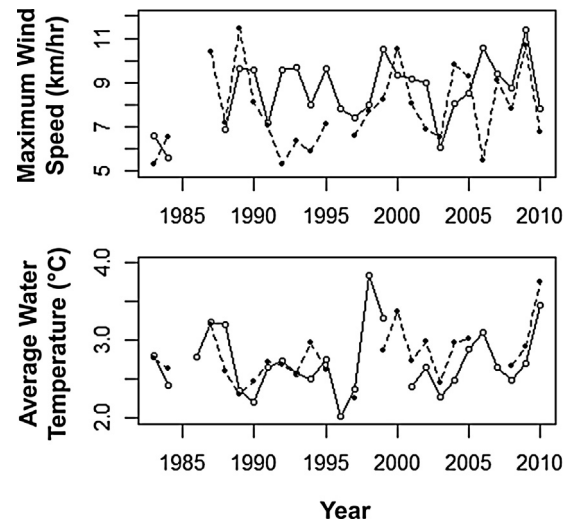


Fig. 8. Time-series of the maximum wind speed (top) and average water temperature (bottom) during spring at the western (dashed line, solid circles) and central (solid line, open circles) offshore NOAA buoys in Lake Superior. Years with no data are missing.

environmental factor (or combination of factors) that exhibits measures of synchrony greater than or equal to the scale of cisco recruitment synchrony (i.e., wind, water temperature) could play a dynamic role in the determination of cisco year-class strength and thus contribute to the broad scale of cisco population synchrony within the Upper Great Lakes region.

Freshwater ecosystems appear to be especially sensitive to changes in climate as these systems are often characterized by distinct seasonal patterns in physical and biological processes. Anthropogenic climate change has caused Lake Superior summer surface water temperatures to increase approximately 2.5 °C during the period of 1979–2006 (Austin and Colman, 2007), which is significantly greater than the rate of regional atmospheric warming. In addition, Desai et al. (2009) argued that increasing air and surface water temperatures could be causing the observed increase in average wind speeds due to the destabilization of boundary layers, which allows energy from winds aloft to be transferred to the lake surface more efficiently. As a result, surface wind speeds are increasing by nearly 5% per decade, which is again greater than the trends in wind speeds over land (Desai et al., 2009). These alterations to the physical environment could have a profound influence on trophic interactions, as even subtle changes in temperature can decouple species from favorable growing conditions (Cushing, 1990). Höök et al. (2006) provided evidence that current velocities in the Great Lakes can far exceed larval fish swimming capabilities, leading to the displacement of larvae from favorable nursery habitat. Similarly, Zhao et al. (2009) used a three-dimensional hydrodynamic-ecological model to demonstrate that wind-driven currents can have a negative impact on walleye recruitment in the western basin of Lake Erie. Our findings suggest that a windier environment could also have a negative influence on age-0 cisco, so we suggest that fisheries managers and scientists (1) pay close attention to cisco recruitment patterns in coming years and (2) consider the use of physical–biological models as a means of investigating the mechanisms that drive recruitment.

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